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Analysis and Modeling of the Root System Architecture of Winter Wheat Seedlings

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Abstract

Plant root system plays an essential role in the acquisition of the edaphic resources, which are subject to local depletion. The size as well as the architecture of the root system determines the efficiency of the acquisition. In the present study, a stochastic model of plant root system architecture is formulated. The continuous growth and development of root system is described and modelled by stochastic processes (discrete events associated with a certain probability). The parameters of the model for each growth cycle include branching probability, w (rhythm ratio main axis vs. lateral roots), b (probability of growth) and c (probability of survival). Root segments were presented as connections of individual nodes. As root has no nodes in the sense of the botanical terms, an imaginary node with an elementary length is introduced.

In order to obtain the parameters of the model, winter wheat seedlings were grown in a phytotron in sand culture watered by nutrient solution. Individual roots of 19-days-old seedlings were scanned and the images obtained were analysed with a root image-analysing software WinRhizo.

Roots were clustered into 3 relatively homogeneous groups after an analysis of similarity according to 4 criteria: length of main axe, diameter of root apex of the main axe, lateral length density (total length of lateral roots per unit of main axe length), lateral root density (number of lateral roots per unit of main axe). In each root group, the parameters were fitted with a non-linear generalised least square method by comparing the theoretical length of root segments of various orders with the experimental data.

Keywords: root system architecture, stochastic model, winter wheat

1 Introduction

The plant root system constitutes the interface of plant-soil and plays an essential role in the acquisition of the edaphic resources such as water and nutrients. As these resources are heterogeneously distributed in soil and subject to local depletion [1, 7], the exploration and exploitation capacities of root system determine the efficiency of the resource acquisition. The exploration capacity of the root system, expressed as the root length density (root length per unit of soil volume, $\text{m}\cdot\text{m}^{-3}$), has a major effect on the dynamics of nutrient depletion and should be taken into account in any prediction of the uptake by roots [18]. The root system

architecture, in his turn determines the exploitation capacity. Root system architecture has several aspects: root typology, topology (spatial relationship of elements of the root system), geometry of root elements and their spatial distribution in soil [12]. Roots of different orders play different roles in absorbing (radially) and transporting (longitudinally) water and nutrients [5]. Root segments of different ages have distinct internal structure and different absorbing capacity and physiological activity [11, 14, 20].

Formalisation of growth and developmental rules is a prerequisite for architectural modelling [2, 8, 16]. In an opaque soil medium, continuous observation necessary for the growth rate determination are difficulties to perform. The primary root system of wheat is made up of more than 10 axial roots with many irregular ramifications, and the absence of morphological mark makes it impossible to determine if a root segment is alive. All this makes the parameters difficultly obtainable.

Objective of the present investigation are: 1 to define typology of the roots of wheat seedlings, and separate the roots into relatively homogenous groups: 2 to formulate a mathematical model describing the root architecture with only a few parameters.

2 Model Description

The model is based on the thesis of De Reffye [4] and the AMAP model (analysis and modeling of architecture of plants) developed by De Reffye and his colleagues [9]. Root system is presented as connexion of root segments of different ages.

Terminology

Cycle : An accumulated temperature-based period, at each cycle of growth all the tips of the root structure can grow, rest or die, if a growth event occurs, an elementary length (described later) will be added to exiting root segment.

Physiological age: Each branching order of a root structure has its own behavior, corresponding to a particular state of development characterized by a series of biological criteria. This characteristic of the structure is called "physiological age", "biological age", "ontogenetic age" or "state age". Generally, the physiological age of axes increases with their ramification order, although all the laterals of the same order do not have necessarily the same physiological ages.

Substructure: substructure is a recursive concept. In root system architecture, each substructure bears a number of root axes having the physiological age 1 unit greater than it, and the composing roots axis are, in their turn, substructures composed of other root axis with more great physiological age. By using the substructure method, the CPU-time to simulate a complex root system is greatly reduced.

Discretization of root axis into elementary length unit

In the root system, there is no morphological markers similar to those present on the above-ground part, i.e. internodes delimited by leaves and auxiliary buds, we have to adopt an imaginary root node concept. In case of a growth event, a segment corresponding to an imaginary node length is added to the root axis. Our imaginary node is similar to the "fundamental distance" in the space separating lateral roots of tomato [15]. This virtual internode is a discretization of the continuous growth. It is empirically set in order to minimize the number of axillaries roots branched on it that cannot be bigger than one, and the number of successive branched (and unbranched) elementary length unit are

geometrically distributed [10]. So its length is close to the minimum average distance between two successive axillary roots branched on an axis. Root axes of different order may have distinct node unit lengths.

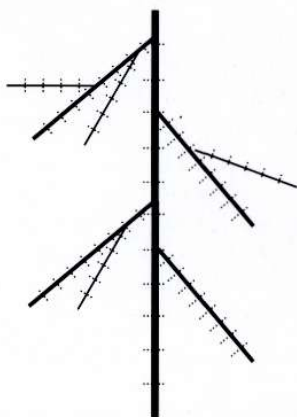


Fig.1 Root branching and imaginary nodes

Root segments are divided into imaginary internode with an elementary length unit. Main and lateral axes of different order have different elementary length units.

Parameters of the model for growth process

w : rhythm ratio, reciprocal of the ratio between the number of functioning cycles allocated to laterals and the number of cycles allocated to bearing axis.

c : probability of survival, the probability for an apical meristem to remain alive in a cycle

b : probability of growth. In a functioning cycle, the growth may occur, there will be an increment of an internode, the probability associated is noted by b , and the probability of dormancy is $1-b$.

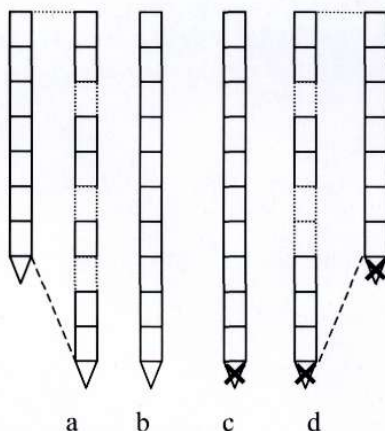


Fig.2 Schematic presentation of root segments. Each rectangle or triangle represents respectively an imaginary node and root apex. The total cycle number is 11. For the root segment a and d , the dotted rectangles represent a virtual node (during the certain cycles the growth has not occurred), there are only 7 observed nodes. The apex with a cross means the root segment is dead

Branching of root axis

The branching process is modelled by a two-states first order Markov chain (Jourdan et al., 1995).

The number of successive imaginary nodes being in the same state (branched and unbranched) are geometrically distributed, and preliminary experiment showed that the lateral roots were distributed along the bearing axis in a random pattern the, i.e. the state of a node is independent of that of the previous one (data not shown).

Growth and development process

At the beginning, we assume that the main root has a probability of growth $p_1=1$. The number of cycles for the laterals of first order has a truncated geometric distribution. Let the total cycles be N , the probability to have L living cycles is:

$$\begin{aligned} p_L (L < N) &= (1-c)c^L \\ p_N &= c^N \end{aligned} \quad (1)$$

The mean and variance of the number of cycles of the lateral are:

$$\begin{aligned} \overline{n_N} &= c \frac{1-c^N}{1-c} \\ \overline{v_N} &= \frac{c}{(1-c)^2} (1-c^N (2N+1)(1-c) - c^{2N+1}) \end{aligned} \quad (2)$$

The probability to reach a length of L imaginary nodes is :

$$p_c(x=L) = \sum_{i=L}^{N-1} (1-c)c^i C_i^L b^L (1-b)^{i-L} + c^N C_N^L b^L (1-b)^{N-L}$$

The first term of the right part of the formula deals with all the dead segments, and the second one with the segments that are still alive.

The root segment at k internodes from the apex on the main axis has k cycles (as we assume the main axis has a probability of growth $p_1=1$), and the lateral root at this position has $w(k)$ cycles, with the following mean and variance:

$$\overline{n_k} = c \frac{1-c^{w(k)}}{1-c} \quad (3)$$

$$\overline{v_k} = \frac{c}{(1-c)^2} (1-c^{w(k)} (2w(k)+1)(1-c) - c^{2w(k)+1}) \quad (4)$$

The mean and variance of the lateral length on the position k of the main axis are functions of w , b and c :

$$M(k) = \overline{n_k} b = b c \frac{1-c^{w(k)}}{1-c} \quad (5)$$

$$V(k) = b(1-b)c \frac{1-c^{w(k)}}{1-c} + b^2 \frac{c}{(1-c)^2} (1-c^{w(k)} (2w(k)+1)(1-c) - c^{2w(k)+1}) \quad (6)$$

Parameter estimation

As described above, the theoretical means and variances of the lateral length on the position k of the main axis are function of w , b and c . The theoretical values of the mean and

variance of the length of first order lateral root, mean and variance of the total length of the second, tertiary order lateral roots were compared with corresponding experimental data, a non-linear least square procedure was performed to fit the parameter w , b , and c .

For a root axis, at each imaginary node, there is only one, if any branch exists. The root system of wheat seedling of 19-day-old consisted of 8 to 14 main root axis. All the branches at the same position on the main axis of all the plant sample were combined to form a theoretical axis. At k virtual internodes from the top, the possible number of cycles follows a negative binomial law, induced from the growth probability b_1 of the main axis. So the lengths of the secondary roots branched at k internodes on the main axis, follows a compound distribution. At each node (k) from the apex along the main axis, the mean $M(k)$ and variance $V(k)$ of branches were calculated and associated with a weight $w(k)$ corresponding to the number of branches at this position. If there was no data at this place (branch number <1 for mean, or 2 for variance), then $w(k)=0$.

If two physiological ages are considered, b_1 , b_2 , c_1 , c_2 , w_2 (by definition $w_1=1$) need to be estimated by least square method. If only alive axis were taken into consideration, $c_1=1$ (viability =1). A few root axes were not included in the sample for computing, as the length of some branches exceeded that of the portion from the branching point to apex of bearing axis. In this instance, either these apexes were dead, or the long branches were reiterations (a special case to be studied in the future). Thus it remained only 4 parameters to be fitted: b_1 , b_2 , c_2 , w_2 . The GLSQR cannot estimate all of them at one time. So they were calculated 2 by 2, at each step, the obtained values served the departure for the estimation of other parameters. The process ended when the same value were always found. The parameter b_1 , b_2 , c_2 , w_2 calculated from roots of wheat seedling were respectively 0.75, 0.305, 0.948 and 1.0. The second visual validation was to simulated roots with that obtained in experiments.

Simulation procedure

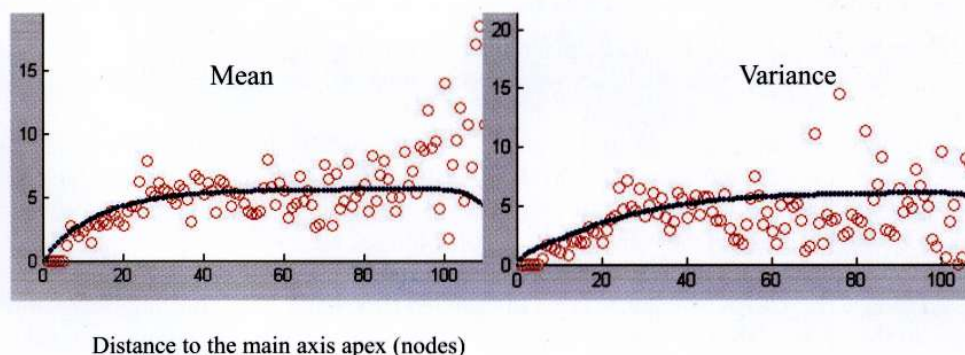


Fig.3 Mean and variance of length of roots of first order lateral along the main axis. Dots: means and variances of the observed data; lines: theoretical means and variances of the simulated data

3 Experimentation Aspects

Winter wheat (*Triticum aestivum*) seedlings were grown in a culture room on sand passed a 2 mm sieve in PVC column of 45 cm height and 10 cm in diameter. There were 4 plants per

column. The bulk density in the column is 1.64 g cm^{-3} . The seedlings were watered once every 3 days with either a complete nutrient solution. The nutrient solution is adapted for monocot plants with the following composition: K_2SO_4 0.75 mmol/L, $\text{MgSO}_4 \cdot 7\text{H}_2\text{O}$ 0.65 mmol/L, KCl 0.1 mmol/L, $\text{Ca}(\text{NO}_3)_2 \cdot 4\text{H}_2\text{O}$ 2.0 mmol/L, KH_2PO_4 0.25 mmol/L, H_3BO_3 1.0 $\mu\text{mol/L}$, $\text{MnSO}_4 \cdot \text{H}_2\text{O}$ 1.0 $\mu\text{mol/L}$, $\text{ZnSO}_4 \cdot 7\text{H}_2\text{O}$ 1.0 $\mu\text{mol/L}$, $\text{CuSO}_4 \cdot 5\text{H}_2\text{O}$ 1.0 $\mu\text{mol/L}$, $(\text{NH}_4)_6\text{Mo}_7\text{O}_{24} \cdot 4\text{H}_2\text{O}$ 0.05 $\mu\text{mol/L}$, EDTA-Fe 0.1 mmol/L. The day and night cycle in the culture room is 11h/14h, with daytime light intensity of $2000 \mu\text{mol}_{\text{PAR}} \text{ m}^{-2} \text{ s}^{-1}$.

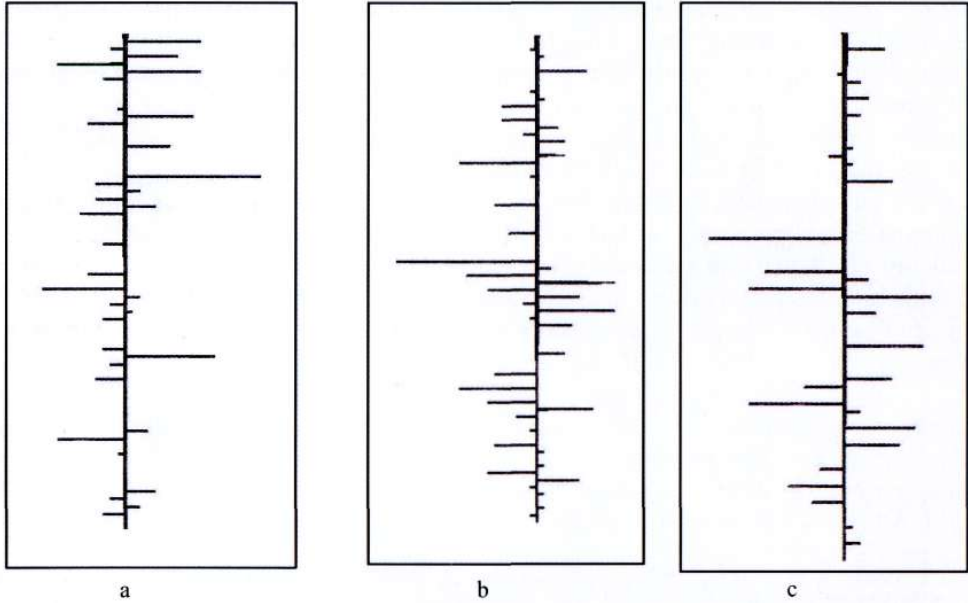


Fig.4 Simulated roots of 90 cycles with the following parameter $b_1=0.8$, $b_2=0.3$ et $c_2=0.96$, $w_2=1.0$

Nineteen days after germination, plants were taken out off the columns carefully to prevent the root from breaking. Roots were removed one by one with their position on the plant noted.

Roots were washed free from sand, and put into a 20 cm*25 cm rectangle Plexiglas box with a layer of 0.5-1.0 cm water. The presence of water layer was necessary to disperse the fine and ramified roots. In a transparency lighting mode, the roots were scanned with a resolution of 400 dpi, and the resulted gray-leveled images were saved in tiff (tagged image file) format. The resulted images were analyzed manually with WinRhizo software (Reagent Instruments Com, Ca) to obtain the length of each lateral and the distance from the insertion point to the apex of their respective bearing axis. Length and distance were expressed as number of imaginary nodes as previously described.

Clustering analysis and root typology

Seedlings with 8 to 12 roots (a very few plants with more than 12 or less than 8 roots were not included in the analysis) were selected to analyse the similarity among the roots. For the complete and P-deficit nutrient solution, the number of plants analysed were respectively 41 and 39. The length and apex diameter (measuring at 0.5 cm from the apex) of the main axis, lateral density (number of 1st order laterals per unit length of main axis),

lateral length density (total length of 1st order laterals per unit length of main axis) were used as criteria for a non-systematic clustering analysis with SPSS software. The analysis showed that when roots were classed into three categories, the differences of the 4 characteristics among categories were highly significant. The clustering of the root coincide with their position (Fig.5), i.e. most members of the category I belong to the seminal radicle and 1st and 2nd pair of adventitious roots, the category II corresponds to 3rd m and 4 th pair, the category III the 5 th and 6th pair of adventitious roots.

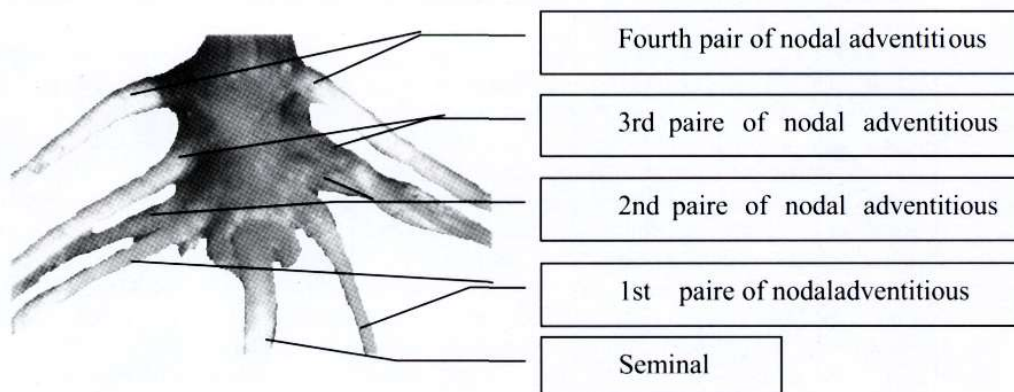


Fig.5 Positions of roots of wheat seedling (after Ma [13])

4 Discussion

Our model describes the growth and development process of apparently very complex root systems although it does not explain the underlying biological phenomena. The advantage is that it is not necessary to know if a root segment is dead or still alive, and the non-linear least square procedure fits the parameters of the model. The simulated root images look like scanned root images. The output of our modeling and simulation includes length of roots of different orders, the total number of root apex. The mean and variance of the length did not differ from that of the measured root data from which the parameters were estimated.

Varney and Canny [19] reported that 80% of water and solute are absorbed by lateral roots. Different parts of root may have different absorbing capacity and number of apex is a characteristic particular relevant to phosphatase secretion [17], and the later is very important for the organic phosphorus hydrolysis. The next studies will compare the root systems that will have different treatments such as phosphorus deficiency. The effect on the root architecture should be reflected by change of the parameters values that control the root system simulation.

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